FOSSIL GROUSE OF THE GENUS *DENDRAGAPUS*

JOSEPH R. JEHL, JR.

ABSTRACT. — Osteological variation in the Pleistocene and Recent populations of *Dendragapus* is reviewed. Two species of *Dendragapus* are recognized from late Pleistocene deposits of the western United States. *Dendragapus lucasi*, which was smaller than the extant *D. obscurus*, and *D. g. gilli*, a large, heavy-bodied grouse, are known only from Fossil Lake, Oregon. *D. nanus*, also described from the Fossil Lake deposits, is considered a synonym of *D. lucasi*. Another grouse, known from cave deposits of northern California, is tentatively described as a small, southern subspecies of *gilli*, *Dendragapus gilli milleri* n. subsp. Phylogenetic relationships between the Pleistocene grouse and *D. obscurus* are not currently resolvable.

Grouse of the genus *Dendragapus*[1] are not common in the fossil record. Three forms, *Dendragapus lucasi* (Shufeldt), *D. nanus* (Shufeldt), and *D. gilli* (Shufeldt) are known only from late Pleistocene deposits at Fossil Lake, Lake County, Oregon. These fossils seem to have been collected from a narrow series of beds with a maximum age of approximately 29,000 years (Allison, 1966). Abundant material referred to the extant Blue Grouse, *D. obscurus*, was reported by Miller (1911) from the Samwel and Potter Creek cave deposits of Shasta County, California. These deposits are of Upper Pleistocene age, but they have not been precisely dated. The locations of the Pleistocene deposits are shown in Figure 1. *Dendragapus obscurus* has also been reported from an Indian midden in the Puget Sound region, Washington (Miller, 1960), and from the Weiss and Birch Creek Valley rock shelters in Idaho (Miller, 1963). Carbon 14 dating indicates a maximum age of 10,000 to 12,000 years for the Idaho remains.

For an earlier study (Jehl, 1967) it was necessary to assemble most of the Fossil Lake *Dendragapus* material previously studied by Howard (1946), the largely unstudied California cave fossils, and a large series of skeletons of modern *D. obscurus*. Because osteological variation in *obscurus* proved to be greater than had been recognized previously, I restudied the differences on which the fossil species had been based in light of this variation. In this paper I review the fossil populations of *Dendragapus* and I attempt to outline their possible relationships to each other and to *D. obscurus*.

MATERIALS

I examined the following skeletal material representing seven of the eight currently recognized races (A.O.U., 1957) of *Dendragapus obscurus*: *D. o. richardsoni*, 1 complete and 2 partial females, 3 complete males; *D. o. pallidus*, 1 complete and 2 partial females, 1 complete male; *D. o. oreinus*, 3 complete and 2 partial females, 1 complete and 1 partial male; *D. o. fuliginosus*, 5 complete females, 4 partial males; *D. o. sitkensis*, 1 partial female; *D. o. sierrae*, 3 complete and 3 partial females, 5 partial males, 1 unsexed; *D. o. howardi*, 3 partial males. Fossil material examined is indicated below under "Referred material" and includes all known material from Fossil Lake examined

[1]Short (1967) has recently proposed that *Canachites* and *Falcipennis*, genera recognized by Peters (1934), be placed in an expanded genus *Dendragapus*. In this paper I use *Dendragapus* in its traditional sense. However, except for a single report of *Canachites canadensis* from the late Pleistocene of Virginia (Wetmore, 1962: 7-8) there is apparently no fossil record of either *Canachites* or *Falcipennis* (Brodkorb, 1964).

SAN DIEGO SOC. NAT. HIST., TRANS. 15 (12): 165-174, 12 FEBRUARY 1969

by Howard with the exception of two elements of *D. lucasi* (1 coracoid, 1 tarsometatarsus) in the Oregon State University collections (Howard, 1946: 179).

The following abbreviations are used: AMNH, American Museum of Natural History: UCMP, University of California Museum of Paleontology; UMMP, University of Michigan Museum of Paleontology.

Figure 1. Pleistocene localities of *Dendragapus* remains.

Identification of Dendragapus *material.* — Howard (1946: 179) has correctly emphasized that there is great variation in the bones of modern species of grouse, which may lead to difficulty in identifying fossil material. *Dendragapus* bones are no exception, and there are few characters by which individual elements of this genus can be distinguished from those of *Pedioecetes, Tympanuchus,* and *Centrocercus.* The humeri, femora, tibiotarsi, and carpometacarpi of *Dendragapus* are more robust than those of the other named genera. The ulnae are heavier and more strongly curved. The tarsometatarsi are somewhat more distinct; the shaft averages wider, the anterior metatarsal groove shallower and less elongated, and the trochleae heavier. The coracoids are similar to those of the other genera, but the antero-ventral process of the furcular facet, in ventral view, is thicker, blunter, and less recurved toward the shaft.

Races of modern *Dendragapus obscurus* are based largely on color variation (Friedman, 1946: 69), though there is an eight to ten per cent difference in wing lengths between the largest and smallest races. Too few skeletons are available for the races to be characterized osteologically. However, I can detect no racial differences in the skeletons at hand. All show the robustness characteristic of the species, and there is no demonstrable geographic variation in robustness.

Dendragapus FROM FOSSIL LAKE

Shufeldt (1892) described two species of grouse from Fossil Lake, Oregon, *lucasi* and *nanus*, which he assigned to the genus *Pedioecetes*. Howard (1946) reassigned both species to *Dendragapus* on the basis of tarsal characters. Other characters, namely the stoutness of the carpometacarpi and the shape of the furcular facet, confirm her reallocation. Shufeldt (1892) erected a new genus, *Palaeotetrix*, for a third species, *gilli*, but this genus is not separable from *Dendragapus* (Jehl, 1967).

Dendragapus lucasi

Among the galliform birds present in the Fossil Lake deposits, this species was second in abundance only to the Sage Grouse (*Centrocercus urophasianus;* Howard, 1946). *Dendragapus lucasi* was somewhat smaller than modern *D. obscurus. All elements*, except one slightly shorter tarsometatarsus, fall within the size range and proportions of *female D. obscurus.* There is marked sexual size dimorphism in grouse, with males averaging larger than females. The apparent small size of *lucasi* probably is not an artifact of sampling, however, as it is unlikely that a sample of 20 elements from at least six individuals was derived entirely from female birds.

The ulna, coracoids, humerus, carpometacarpi, and femur of *lucasi* are indistinguishable from those of female *obscurus.* Howard (1946: 180) suggested two characters, "relatively less depth of proximal end and less development of the intermetacarpal tuberosity," by which carpometacarpi of *lucasi* were thought to differ from those of *obscurus.* However, she presented no quantitative data in support of the first character, and I find that the great variation in the large series of *obscurus* at hand encompasses that exhibited by elements assigned to *lucasi.* Furthermore, in *obscurus* the development of the intermetacarpal tuberosity is perhaps the most highly variable feature of the carpometacarpus; the development of this structure in *lucasi* is quite within the range of variation exhibited in *obscurus.*

The tarsometatarsi of *lucasi* are also extremely similar to those of *obscurus* but show several minor average differences: the metatarsal facet is smaller and more clearly defined proximally; the area below the internal cotyla on the posterior face is less deeply excavated; and the ridge bordering this depression, running between the internal cotyla and the metatarsal facet, is less well defined. The trochleae average smaller than in *obscurus*, but the symmetry of the distal end of the tarsometatarsus and the position of the internal trochlea (cf. Howard, 1946: 180) are within the range of variation of *obscurus.* Also, I detect no difference in the depth of the internal edge of the shaft, nor in the depth and prominence of the hypotarsus (cf. Howard, 1946). The morphology of the hypotarsus is somewhat variable in *obscurus* and includes the variation exhibited by *lucasi.*

In summary, *Dendragapus lucasi* may be characterized as a Pleistocene *Dendragapus* differing from the modern *D. obscurus* only in over-all size and in minor characters of the tarsometatarus.

Referred material. — Ulna-1 (AMNH no. 3476, Type). Carpometacarpus-7 [UCMP no. 31748, previously tentatively referred to *D. nanus*, see explanation below; AMNH nos. 3475A (2), 3477A (2), 3478A (2)]. Tarsometatarsus — 8 [AMNH nos. 3475 (2), both previously referred to *D. nanus*; 3475A (4), 3476 (2)]. Coracoid — 2 [AMNH no. 3478A (2)]. Humerus — 1 (AMNH no. 3478A). Femur — 1 (UCMP no. 31781). Tentatively referred. — Radius — 1 (UCMP no. 31776).

Dendragapus nanus

According to Shufeldt's (1892: 414) original description *D. nanus* differed from *D. lucasi* "only in the matter of size," *nanus* being smaller. However, this distinction is no longer valid. Howard (1946) reassigned four tarsometatarsi and two carpometacarpi from *nanus* to *lucasi*, retaining only two tarsometatarsi (AMNH no. 3475) and, tentatively, one carpometacarpus (UCMP no. 31748) in *nanus*. All of these elements are within the size range of *D. lucasi*.

Howard (1946) considered the carpometacarpus of *nanus* to differ from those of *obscurus* (and, by implication, from those of *lucasi*) in having "the external surface of the proximal end . . . less rugose and the process of metacarpal I . . . more markedly tilted upward." However, I could not confirm these differences when I compared the carpometacarpus of *nanus* with a large series of *obscurus*. Tarsometatarsi of *nanus* were said to resemble those of *obscurus*, and consequently to differ from those of *lucasi*, by having a "short, prominently projecting hypotarsus." As noted above, variation in the hypotarsus in *obscurus* is too great to make this character of diagnostic value. Howard also stated (p. 180) that tarsi of *nanus* differed from those of *obscurus* by the "(1) extreme proximal location of tubercle for tibialis anticus muscle; (2) more symmetrically flared distal end; and (3) relatively more slender shaft." Again, variation in *obscurus* includes the differences by which *nanus* was distinguished. In some *obscurus* the position of the tubercle is as far proximal, and in one *lucasi* it is more proximal; the symmetry of the distal end is variable and some tarsi of *obscurus* match those of *nanus* exactly; the ratio of least lateral width of the shaft to total length of the tarsometatarsus does not indicate that the element was slenderer in *nanus* than in *obscurus* (Table 4).

In summary, I find no characters except smaller size that allow elements previously assigned to *D. nanus* to be differentiated from *D. obscurus*. Unfortunately, the sample of *nanus* is too small to indicate whether the tarsal characters that seem to distinguish *lucasi* from *obscurus* may also separate *lucasi* from *nanus*. However, these differences are slight, and I believe, judging from the variation in tarsal characters both in *obscurus* and in the California cave material discussed below, that the tarsal elements assigned to *nanus* are within the range of variation of *lucasi*.

Because of the similarity of grouse elements from different species and the great variation within species, it is impossible to disprove the occurrence of two small species of *Dendragapus* in the Fossil Lake beds. Nevertheless, the characters that have been used to differentiate *D. nanus* do not allow it to be separated from either *D. lucasi* or females of *D. obscurus*. I would, therefore, withhold specific recognition from *nanus* and consider it synonymous with its contemporary, *lucasi*, with which it agrees in size and proportions, rather than with the slightly larger and (apparently) more recent *obscurus*.

Dendragapus gilli

This large grouse, which approximated in size females of *Centrocercus urophasianus*, is currently known only from two carpometacarpi (AMNH no. 3474, type; UMMP no. 48223). *D. gilli* differs from *obscurus* and *lucasi* only in size and robustness, but in these characters it is completely separable. As no carpometacarpus of *lucasi* or even of *obscurus* males attains the great size and robustness that appears to characterize *gilli*, the latter must be considered specifically distinct.

THE CALIFORNIA CAVES POPULATION

Remains of Pleistocene *Dendragapus* are abundant from the Samwel and Potter Creek caves of Shasta County, California. Loye Miller, who first reported these fossils (1911: 396-397), assigned most to *D. obscurus*, but suggested that more than one species might be represented for many bones were of "unusual size" and "great robustness" and differed by "slight detail of the head of the tarsometatarsus." Miller was unable to analyze these fossils, because of a lack of modern skeletal material. (Nearly 60 years later complete skeletons of male *obscurus* are still in too short supply.) In examining this material I detected only one form of *Dendragapus;* there were no demonstrable differences between Samwel and Potter Creek cave specimens. However, this form differed in body size and relative stoutness of the long bones from other *Dendragapus.* A discussion of individual elements follows.

Carpometacarpus. — Except for greater robustness, carpometacarpi of the California cave grouse are indistinguishable from those of *lucasi* or *obscurus;* they are as robust, but not as long, as those of *gilli* (Table 1). The shape of the distal portion of metacarpal III is highly variable and does not, as might be inferred from Figure 2, offer a valid means of distinguishing this form.

Referred material: UCMP nos. 5401, 5621, 8926, 8910a, 9621 (2), 9621a, 9743, 10043, 10160, 10183 (5), 27312 (2), 82977. *Tentatively referred:* UCMP nos. 27322, 27322a.

TABLE 1
MEASUREMENTS OF CARPOMETACARPUS IN *Dendragapus* (IN MM)

Species	No.	*Total length* *Range and Mean*	S.D.	No.	*Width metacarpal II* *Range and Mean*	S.D.	No.	*Ratio, width metacarpal II to length carpometacarpus × 100* *Range and Mean*	S.D.
D. obscurus ♂	7	38.8-42.5 (40.6)	1.6	5	4.1-4.3 (4.2)		5	10.1-10.7 (10.4)	.18
D. obscurus ♀	20	34.3-39.4 (36.7)	1.2	20	3.3-3.9 (3.6)	.18	20	8.8-10.9 (99)	.43
Samwel and Potter Creek cave fossils	15	34.3-40.0 (36.2)	1.7	15	3.7-4.4 (4.0)	.20	15	10.5-11.8 (11.3)	.38
D. lucasi	7	34.3-39.3 (36.9)	1.5	7	3.4-4.0 (3.7)	.23	7	9.9-10.8 (10.2)	.30
D. gilli	2	43.8, 45.1		2	5.2, 5.2		2	11.5, 11.9	
"*D. nanus*"	1	38.5		1	3.8		1	10.0	

Ulna. — The ulnae average slightly longer than those of female *obscurus* and the shafts average approximately five per cent wider (Table 2). Some shafts appear slightly less curved than in *obscurus.*

Referred material: UCMP nos. 3922, 8910a, 8926a (2), 8789, 9528, 9554e, 9556, 9728, 9746, 27312, 27313, 27322, 27322a, 31758. *Tentatively referred:* UCMP nos. 3049, 3608, 9554c (2), 9554d, 10119 (3), 27322a, 31737 (6).

TABLE 2
MEASUREMENTS OF ULNA IN *Dendragapus* (IN MM)

Species	No.	*Total length* *Range and Mean*	S.D.	No.	*Proximal width (tip of olecranon to tip of external cotyla)* *Range and Mean*	S.D.	No.	*Greatest distal width* *Range and Mean*	S.D.
D. obscurus ♂	9	65.5-71.0 (67.6)	1.4	9	12.5-14.0 (13.5)	.46	9	9.6-10.8 (10.1)	.39
D. obscurus ♀	19	57.9-64.8 (61.6)	1.8	20	11.2-12.9 (12.2)	.40	20	8.4-9.4 (9.0)	.31
Samwel and Potter Creek cave fossils	9	59-67 (62.8)	2.4	1	11.8		10	8.8-10.1 (9.1)	.41
D. lucasi (type)	1	63.9		1	11.5		1	8.7	

TABLE 4

MEASUREMENTS OF TARSOMETATARSUS IN *Dendragapus* (IN MM)

Species	No.	*Total length* Range and Mean	S.D.	No.	*Ratio, least lateral width shaft to total length × 100* Range and Mean	S.D.	No.	*Greatest proximal width* Range and Mean	S.D.	No.	*Greatest width across trochleae* Range and Mean	S.D.	No.	*Least lateral width shaft* Range and Mean	S.D.
D. obscurus ♂	9	43.3-49.3 (45.5)	2.3	9	9.4-11.2 (10.2)	.59	9	10.1-12.4 (11.0)	.69	8	11.2-12.4 (11.8)	.44	9	4.2-5.2 (4.7)	.30
D. obscurus ♀	18	38.1-44.7 (41.7)	1.9	18	8.6-10.9 (9.7)	.67	17	8.9-10.2 (9.6)	.59	18	9.5-11.6 (10.6)	.54	18	3.6-4.4 (4.0)	.24
Samwel and Potter Creek cave fossils	11	36.7-44.3 (41.3)	2.1	12	8.8-11.2 (10.4)	.70	14	9.3-10.8 (9.8)	.19	15	9.6-11.5 (10.7)	.12	32	3.7-5.2 (4.4)	.39
D. lucasi	5	37.8-43.5 (40.1)	1.3	4	9.1-10.5 (9.8)	.58	4	9.0-9.4 (9.2)	.19	4	9.6-10.0 (9.9)	.21	4	3.6-3.9 (3.8)	.17
"*D. nanus*"	1	38.9		1	9.9		2	9.5, 9.6		1	10.2		2	3.8, 3.9	

Humerus. — Most of the humeri are fragmentary and lengths can be obtained or estimated for only five specimens; only one of these falls beyond the length of *obscurus* females. The humeri appear to have slightly smaller heads and the shafts are slightly straighter distally, averaging approximately eight per cent wider than in *obscurus* (Table 3).

Referred material: UCMP nos. 4096, 4275, 4281, 5287, 5491, 5285, 6774, 6921, 6961, 6962, 8053, 8324, 8910, 9514, 9554a, 9646, 9712, 10147, 10160, 10183, 27312 (2), 27314, 27315 (2), 27342 (3), 27325, 31722.

TABLE 3
MEASUREMENTS OF HUMERUS IN *Dendragapus* (IN MM)

Species	No.	Total length Range and Mean	S.D.	No.	Greatest distal width Range and Mean	S.D.
D. obscurus ♂	14	69.7-75.0 (72.4)	2.1	14	14.4-15.7 (15.8)	.59
D. obscurus ♀	24	61.8-69.5 (65.1)	1.9	25	12.6-14.6 (13.6)	.48
Samwel and Potter Creek cave fossils	5	62.8, 63.5, 64*, 68*, 72.3		7	11.4-14.0 (13.5)	
D. lucasi	1	66.6		1	13.6	

*estimated lengths

Tarsometatarsus. — Tarsometatarsi are similar to those of *lucasi* and of *obscurus* females, but the shafts are noticeably wider (Table 4, Fig. 2). In all other respects including the shape of the head (cf. Miller, 1911: 397), they are within the range of variation of *obscurus.* Compared with *lucasi,* the trochleae are much more robust, the metatarsal facet is less well defined, the depression below the internal cotyla on the posterior face is deeper, and the ridge bordering this depression is more pronounced.

Referred material: UCMP nos. 3580, 4624, 5798, 8505, 8923a, 9554, 9554a, 9634, 9644, 9674, 9729, 9740, 9784, 9790, 9803, 9828, 10183a, 27313, 27323, 27324a, 27324b, 27325a, 31718, 31722, 37662, 37663, 37664, 37665, 37666, 37667, 37668. *Tentatively referred:* UCMP nos. 5501, 7430, 10183.

Tibiotarsus. — The fragmentary nature of most of the tibiotarsi makes detailed analysis impossible. Two nearly complete elements (length estimated) are longer than those of female *D. obscurus.* Shaft widths are approximately five to ten per cent greater than in *obscurus* elements of comparable length; the distal width is also greater (Table 5).

Referred material: UCMP nos. 8873, 8926a, 9554a, 27322, 27323, 27323a, 27323b, 31716, 31722, 31757.

TABLE 5
MEASUREMENTS OF TIBIOTARSUS IN *Dendragapus* (IN MM)

Species	No.	Total length Range and Mean	S.D.	No.	Lateral width across trochleae Range and Mean	S.D.
D. obscurus ♂	12	89.0-97.8 (92.8)	2.6	12	9.7-10.9 (10.0)	.42
D. obscurus ♀	19	78.4-89.2 (84.3)	2.9	17	8.7-10.0 (9.3)	.45
Samwel and Potter Creek cave fossils	5	81.5*, 83.5*, 84*, 91.5*, 91.5*		4	9.9-10.9 (10.4)	

*estimated lengths

Femur. — None of the five femora (UCMP nos. 9554a, 9607, 9710, 9714, 27314) examined are complete, but it is clear that all are within the size range of female *obscurus;* shafts average approximately ten per cent wider than in similarly sized *obscurus* (Table 6).

TABLE 6

MEASUREMENTS OF FEMUR IN *Dendragapus* (IN MM)

Species	*No.*	*Total length* Range and Mean	*S.D.*	*No.*	*Greatest distal width* Range and Mean	*S.D.*
D. obscurus ♂	12	73.8-79.4 (75.6)	2.1	12	13.7-15.5 (14.2)	.65
D. obscurus ♀	22	65.1-71.3 (67.5)	1.9	22	11.6-13.0 (12.3)	.51
Samwel and Potter Creek cave fossils	2	65.5*, 69.0*		1	12.0	
D. lucasi	1	68*				

*estimated lengths

Coracoid. — As far as can be determined, the coracoids fall within the length range for female *obscurus.* Some are wider, but there is not enough material for critical comparison. I have found no method of distinguishing these coracoids from those of *lucasi* or *obscurus.*

Referred material: UCMP nos. 3180, 5836, 7042, 7428, 8926a, 9674, 10160, 31713, 31722, 31759.

TABLE 7

MEASUREMENTS OF CORACOID IN *Dendragapus* (IN MM)

Species	*No.*	*Length from head to tip of sternal facet* Range and Mean	*S.D.*
D. obscurus ♂	13	53.6-59.0 (56.9)	2.5
D. obscurus ♀	26	47.4-54.8 (50.2)	1.9
Samwel and Potter Creek cave fossils	4	48.5*, 49.6, 50.9*, 51.5*	
D. lucasi	2	52.7, 52.9	

*estimated lengths

Other elements: Two cervical vertebrae (UCMP nos. 9521, 10183), three fragments of synsacrum (UCMP nos. 9633, 9674, 9696) and one furculum (UCMP no. 8926a) are similar to those of *obscurus* and are probably referable to this population.

Discussion. — The California cave population was similar to *D. lucasi* in size but differed in greater stoutness of the long bones. Smaller than *D. gilli*, it closely resembled that form in robustness. Compared with the extant *D. obscurus,* the cave grouse was slightly smaller, nearly all elements falling within the size range of *obscurus* females, but the long bones averaged five to ten per cent more robust.

In interpreting these cave deposits the possibility of biased sampling must be considered. If predators responsible for amassing these remains were unable to carry large grouse, the resulting deposits would be composed largely of the much smaller females and much of the variation in the fossil population would be obscured. However, many of the bird and mammal predators known from these deposits (Miller, 1911; Furlong, 1906) could have carried larger birds with ease. I conclude that the differences ascribed to the cave remains are valid and, therefore, that this population is worthy of taxonomic recognition.

The affinities of this population are not obvious. Although some individual bones cannot be distinguished from those of *obscurus,* the California fossil population averaged much stouter than *obscurus.* I detect no geographic variation in robustness in races of *obscurus*, and in other grouse that I have examined robustness of the long bones appears to be a conservative character. For these reasons I infer that the cave grouse probably was most closely related to the similarly robust though much larger *D. gilli*. Even if this inference is correct, the nature of the relationship between these forms can only be surmised, owing to a lack of *gilli* material. The cave form could have been specifically distinct, but it is hard to believe that *three* species of *Dendragapus* occupied so small an area of the west only a few thousand years before the first appearance of *obscurus*. It seems most reasonable to treat this population as a smaller, probably contemporaneous, southern subspecies of *gilli*. I name this population *Dendragapus gilli milleri* in honor of Dr. Loye Holmes Miller, who first called attention to these fossils. The Oregon population thus becomes the nominate race, *D. g. gilli*.

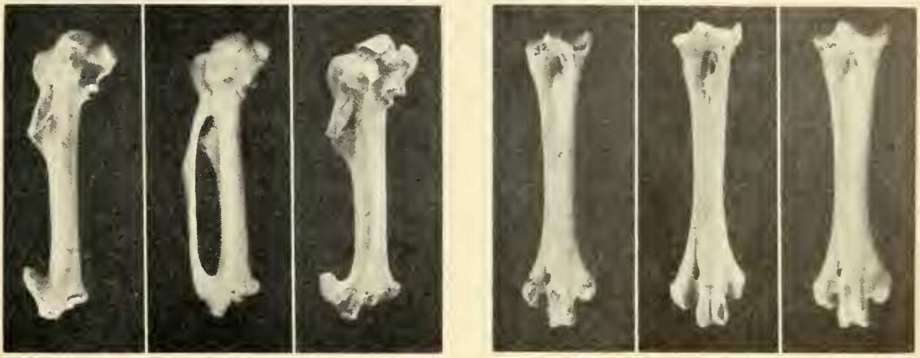

Figure 2. Left to right, carpometacarpi of *Dendragapus lucasi* (AMNH no. 3478A), *Dendragapus obscurus* (UMMZ 74758), *Dendragapus gilli milleri* (UCMP no. 82977); tarsometatarsi of *Dendragapus lucasi* (AMNH no. 3475A) *Dendragapus obscurus* (UMMZ no. 208192), *Dendragapus gilli milleri* (UCMP no. 9823). All illustrations X 1.

Dendragapus gilli milleri new subspecies

Holotype. — Left carpometacarpus, lacking metacarpal III and exhibiting slight wear on distal end. University of California Museum of Paleontology no. 82977 (Fig. 2).

Age and locality. — Late Pleistocene deposits of Samwel Cave, Shasta County, California.

Diagnosis of holotype. — Similar in robustness to carpometacarpi of *D. g. gilli* but approximately 18 per cent shorter; similar in size to carpometacarpi of *D. lucasi* and *D. obscurus* but 10 per cent more robust.

Measurement of holotype. — Total length 38.7 mm; width of metacarpal II at midpoint 4.3 mm; depth of proximal end through process of metacarpal I and internal crest of trochlea 12.4 mm; ratio, width of metacarpal II at midpoint to total length 11.2 per cent.

Referred material. — As discussed above (pp. 169-172).

SYNTHESIS

In the late Pleistocene two species of *Dendragapus* inhabited a small area of the western United States. *Dendragapus lucasi* and *D. g. gilli* occurred sympatrically in southern Oregon; a smaller subspecies of *gilli, D. g. milleri*, occurred in northern California. The relationships of these Pleistocene grouse to the extant *D. obscurus* are not clear. If robustness of the long bones is a conservative character, as I have suggested, *lucasi* would appear to be the most likely ancestor for *obscurus*. *D. gilli* may have become extinct at the end of the Pleistocene, leaving no descendants, but this is far from certain. If "*Dendragapus obscurus*" can be shown to comprise two species (see Friedmann, 1946: 68), *gilli* may have been ancestral to one, *lucasi* to the other. In that event, the problems associated with matching ancestral and descendant populations will be extremely difficult. Until more information is available regarding the distribution and variation in the fossil populations, evolutionary rates, the significance of the differences that characterize the several populations, the temporal relationships of the Pleistocene forms, as well as taxonomic relationships within *D. obscurus*, further speculation on relationship in this genus is best postponed.

Acknowledgments

The late R. A. Stirton, University of California Museum of Paleontology, kindly made the Samwel Cave and Potter Creek Cave material available to me. E. H. Colbert, American Museum of Natural History, loaned specimens of *D. lucasi* and "*D. nanus*," and allowed me to examine type material in his care. Skeletons of *D. obscurus* were obtained through: N. K. Johnson and the late A. H. Miller, University of California; O. M. Buchanan and T. R. Howell, University of California at Los Angeles; R. F. Johnston, the University of Kansas; K. E. Stager, Los Angeles County Museum; and H. G. Lumsden. I am indebted to C. W. Hibbard for advice and assistance throughout this study, to H. B. Tordoff, R. W. Storer, and R. M. Mengel for commenting on an earlier draft of the manuscript, and especially to Hildegarde Howard for her careful and helpful editorial assistance.

Literature Cited

Allison, I. S.
1966. Fossil Lake, Oregon, its geology and fossil faunas. Oregon State University Press. 48 p.

American Ornithologists' Union
1957. Check-list of North American Birds, 5th ed. Lord Baltimore Press, Baltimore, Md.

Brodkorb, P.
1964. Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). Bull. Florida State Mus. 8(3): 195-335.

Friedmann, H.
1946. The Birds of North and Middle America. U. S. Natl. Mus. Bull. 50, Part X. U. S. Govt. Printing Office, Washington, D.C.

Furlong, E. L.
1906. The exploration of Samwel Cave. Amer. J. Sci. 22: 235-247.

Howard, H.
1946. A review of the Pleistocene birds of Fossil Lake, Oregon. Carnegie Inst. Wash. Publ. 551. pp. 141-195.

Jehl, J. R., Jr.
1967. Birds from Fossil Lake, Oregon. Condor 69: 24-27.

Miller, L. H.
1911. Avifauna of the Pleistocene cave deposits of California. Univ. Calif. Publ. Geol. 6: 385-400.
1960. Some Indian midden birds from the Puget Sound area. Wilson Bull. 72: 392-397.
1963. Birds and Indians in the west. Bull. S. Calif. Acad. Sci. 62: 178-191.

Peters, J. L.
1934. Check-list of birds of the world. Vol. 2. Cambridge, Harvard University Press, 401 p.

Short, L. L., Jr.
1967. A review of the genera of grouse (Aves, Tetraoninae). Amer. Mus. Novitates no. 2289, 39 p.

Shufeldt, R. W.
1892. A study of the fossil avifauna of the *Equus* beds of the Oregon Desert. J. Acad. Nat. Sci. Philadelphia 9: 389-425.

Wetmore, A.
1962. Notes on fossil and subfossil birds. Smiths. Misc. Coll. 145(2): 1-17.

Accepted for Publication 13 January 1969

San Diego Natural History Museum, P. O. Box 1390, San Diego, California 92112.